Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem

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The allocation of biomass and nutrients (N, P, K, Ca, Mg) was measured from August 1976 to September 1978 in a young, second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand in the Oregon Coast Range. Tree biomass comprised 78–79% of the total standing crop of organic matter with the remainder allocated as follows: soil organic matter, 17%; forest floor, 4%; and fungi, 2%. Bole biomass accounted for 64–66% of the total tree standing crop; the remainder was apportioned among: nonmycorrhizal roots, 17–18%; branches, 7–8%; mycorrhizae, 6%; and foliage, 4%. Nutrient stocks in aboveground tree components exceeded those in belowground components by one to nine times. For all nutrients except Ca, roots and mycorrhizae contained larger stocks than either the forest floor or fungi; amounts of Ca in the forest floor and in fungi were twice those in roots and mycorrhizae. Return of organic matter to the soil by fine roots and mycorrhizae ranged from 84 to 78% of total tree return. About 73% of total net primary production was invested in growth and maintenance of roots and mycorrhizae. Return of N, P, and K to the soil by mycorrhizae comprised 83–87% of total tree return and 25–51% of Ca and Mg return. Return by mycorrhizae of N, P, and K was four to five times greater than that of roots, nearly equal for Ca, and three times less for Mg.

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Les auteurs ont mesuré l'allocation de biomasse et d'éléments nutritifs (N, P, K, Ca, Mg), durant la période allant de août 1976 à septembre 1978, dans un jeune peuplement de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de la partie côtière de l'Orégon. La biomasse des arbres totalisait 78–79% de la quantité totale de matière organique du système, le reste étant partagé ainsi: matière organique du sol, 17%; couverture morte, 4%; biomasse fongique, 2%. La biomasse des tiges s'élevait à entre 64 et 66% de celle de la population sur pied, le reste étant distribué ainsi: racines non mycorhizées, 17–18%; branches, 7–8%; mycorhizes, 6%; feuillage, 4%. Les stocks d'éléments de la partie aérienne des arbres étaient de un à neuf fois supérieurs à ceux de la partie souterraine. Les racines et les mycorhizes renfermaient, pour tous les éléments à l'exception de Ca, des stocks supérieurs à ceux de la couverture morte ou des champignons; les stocks de calcium de la couverture morte et des champignons totalisaient le double de celui des racines et des mycorhizes. La litière de racines fines et de mycorhizes s'élevait de 84 à 78% de la litière annuelle totale des arbres. Environ 73% de la production primaire nette du peuplement fut pour la croissance et le maintien des racines et des mycorhizes. La restitution au sol de N, P et K par les mycorhizes s'élevait à entre 83 et 87% de la restitution totale des arbres et à entre 25 et 51% de la restitution de Ca et Mg. La restitution de N, P et K par les mycorhizes était de quatre à cinq fois supérieure à celle des racines; elle était à peu près égale pour Ca et trois fois moindre pour Mg.
[Traduit par le journal]

Introduction

Very little is known about the magnitude of the contribution mycorrhizae and fungi make to nutrient cycling in forest ecosystems despite the massive documentation of the importance of fungi in decomposition (Dickinson and Pugh 1974) and of mycorrhizae in mineral nutrition of plants (Fogel 1980). Recently, the first glimmerings of the importance of the belowground ecosystem in nutrient cycling have emerged from studies of fine roots (e.g., Edwards and Harris 1977; Harris *et al.* 1980; McQueen 1973; Ovington and Madgwick 1959; Persson 1978; Reynolds 1975; Santantonio 1979). The studies of fine roots indicate that the majority of organic input to the decomposition process results from fine-root production. One is left, however, with the nagging question of whether the contribution of mycorrhizae has been fully assessed given the efficiency of the methods generally employed to separate fine roots from soil. To complete the picture, one would like to know the relative importance of different fungal components (e.g., mycorrhizae versus litter hyphae) in nutrient cycling.

In an earlier paper (Fogel and Hunt 1979) the rela-

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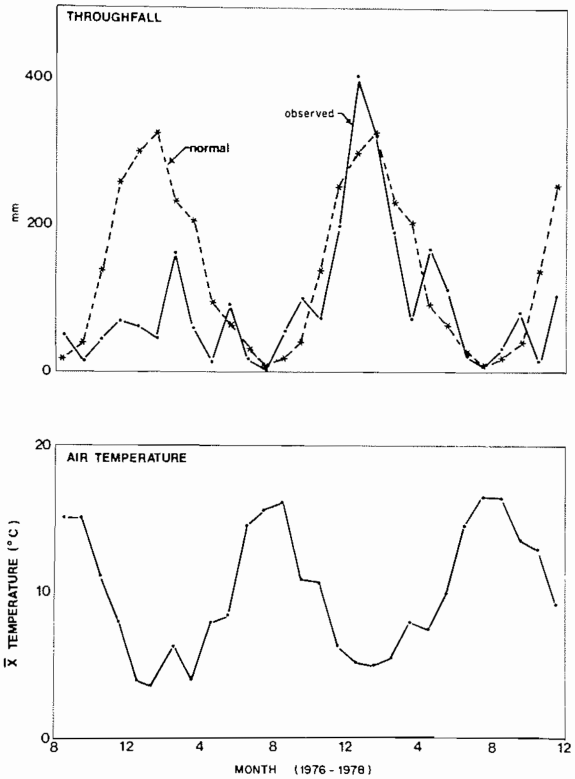

FIG. 1. Air temperature and throughfall precipitation for the Dinner Creek, Oregon, research area.

tive importance of mycorrhizae to carbon cycling in a young second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand was described. Mycorrhizae were shown to account for a major portion of the turnover of organic matter in 1 year when annual precipitation was only 45% of normal. The present paper compares the relative contribution of ecosystem components in the previously reported drought year with that in the year immediately following when precipitation was near normal. The contribution of mycorrhizae, as an inseparable extension of the root system, to net primary production is also reported. Finally, nutrient budgets are presented describing the relative importance of mycorrhizae and other ecosystem components to the cycling of nitrogen, phosphorus, potassium, calcium, and magnesium.

Site description

The investigation was conducted in a second-generation forest of 35- to 50-year-old Douglas-fir located near Philomath, Oregon. The site has been described in detail previously (Fogel and Hunt 1979). The climate of the study area (Fig. 1) is typified by warm, dry summers (July mean temperature 18.5°C) and mild, wet winters (January mean temperature 2.7°C) with little or no snow accumulation. Annual precipitation averages 1905 mm, but fell substantially below average (848 mm) during the 1st year of the study (September 1976 through August 1977) and slightly below (1775 mm) the 2nd year. Maximum predawn plant moisture stress of the overstory reached −13.5 bars (1 bar = 100 kPa) in September 1977 and −9.9 bars in September 1978.

Methods

Standing crops

Methods used to estimate standing crops of ecosystem components and organic matter transfers have been detailed previously (Fogel and Hunt 1979). Arboreal and coarse-root standing crops were calculated from regression formulae developed by Dice (1970) for 36-year-old Douglas-fir in western Washington for 134 sample trees, each standing crop averaged, then multiplied by the number of stems per hectare. Destructive sampling was employed for estimating litter standing crop. Mycelia were quantified by the modified Jones and Mollison soil−agar film technique (Nagel-De Boois and Jansen 1971). The soil core method of Marks *et al.* (1968) was used to measure standing crops of ectomycorrhizae, fine roots, and *Cenococcum geophilum* Fr. sclerotia. Soil organic matter content was determined by the Walkley−Black titration method (Noonan and Holcombe 1975). Litter traps were used to quantify litter input to the forest-floor and the litterbag technique for studying the decomposition of needles and fine roots.

Net primary production

Net primary production (NPP) was calculated by the following equation: NPP $= \Delta B + D + G$ where ΔB is annual biomass increment (uptake *fide* Fogel and Hunt 1979), and D is detritus production or throughput (release and return *fide* Heilman and Gessel 1963). Grazing by herbivores (G) is assumed to be negligible and not considered in the calculations. Whittaker (1975), for instance, estimates that in a temperate deciduous forest the average herbivore consumption of total NPP is less than 0.5%.

Nutrient analyses

Substrates were dried at 60°C and then ground (<0.41 mm) prior to nutrient analysis. Mycorrhizae and sclerotia used for nutrient analyses were not pretreated with sodium pyrophosphate. Total nitrogen was determined by the micro-Kjeldahl method (Jackson 1958). After digestion in perchloric acid, phosphorus was assayed by the molybdate-blue technique (Rand 1976) and cations were determined by atomic absorption spectrophotometry.

Nutrient calculations

Nutrient stocks for each of 2 years were calculated by multiplying the standing crops by the corresponding mean nutrient concentrations. Standing crops were determined by direct measurement, i.e., forest floor, logs, sporocarps, mycorrhizae, hyphae, or by balancing inputs and outputs, i.e., forest floor in year 2. Arboreal standing crops for years 2 and 3 were estimated by determining the correlation between tree ring width measured with a dendrochronometer at 6× and stem dbh, calculating the increment for each of the 134 stems used in the study, adding the increment to the previous year's dbh, recalculating standing crops by using Dice's (1970) formulae, averaging each standing crop, and then multiplying by the number of stems per hectare.

Nutrient uptake (replacement plus increment) was calculated by using measured biomass input, i.e., litter fall, differences between minimum and maximum monthly standing crops, or the difference between year 1 and year 2 standing crops. Throughput (nutrient transfer) was determined by direct measure of the nutrient content of a selected subsample, i.e, litter fall, sporocarps, or by multiplying biomass throughput by the corresponding mean nutrient concentration, i.e., fine roots, sclerotia, mycorrhizae, hyphae. Nutrient concentrations of precipitation, stem flow, soil water, and litter leachate were not measured.

Results and discussion

Several major changes in the presentation of data have been made in this report compared with our earlier paper on the allocation of organic matter among ecosystem components (Fogel and Hunt 1979). The first change is the inclusion of mycorrhizal fungus biomass in the tree rather than the fungal compartment. This change emphasizes the role of mycorrhizae in functionally extending the region of nutrient absorption considerably beyond the 1- to 2-mm zone generally ascribed to roots (Rhodes and Gerdemann 1975). The second change is the addition of fine-root (<5 mm diam.) data, measured subsequent to our earlier report, to the root biomass estimates derived from Dice's (1970) root equation for Douglas-fir roots. The methods employed by Dice (1970) for separating roots from soil certainly exclude a substantial portion of the roots smaller than 5 mm in diameter. Santantonio *et al.* (1977) provide additional support for this position in that root biomass estimates derived by Dice's (1970) equation are similar to the estimates obtained with an equation they developed for Douglas-fir roots larger than 10 mm diameter. Another change has been the calculation of the various standing crops for each of 134 trees prior to averaging and extrapolation to a hectare basis instead of using an average dbh in the allometric equations. This latter change has been made because it has been shown that using an average dbh can result in underestimates of 27–45% in biomass depending on component (Ovington and Madgwick 1959; Baskerville 1965).

No difference exists between year 1 and year 2 in the relative order of allocation of organic matter among compartments at Dinner Creek, although slight differences in individual percentages exist (Table 1). Tree biomass comprises 78–79% of the total standing crop of organic matter. The remainder is allocated as follows: soil organic matter, 16–17%; forest floor, 4%; and fungi, 2%. Bole biomass accounts for 64–66% of the total tree standing crop; the remainder is divided among: roots, 17–18%; branches, 7–8%; mycorrhizae, 6%; and foliage, 4%.

Fine-root and mycorrhiza biomass

Biomass allocation among tree components at Dinner Creek resembles that of other forest stands of similar age in North America (Alban *et al.* 1978; Dice 1970), if mycorrhiza biomass is included in the soil rather than the tree compartment. The nonmycorrhizal root biomass value of 17–18% of total tree biomass falls within the general range of 15–25% of tree biomass reported for a number of forest ecosystems (Assmann 1970; Harris *et al.* 1980; Rodin and Basilevich 1967).

Resolution of the question of whether mycorrhizae have been included in biomass estimates is crucial to understanding nutrient cycling in forest ecosystems given the large input of mycorrhizae to the decomposition process (Fogel and Hunt 1979). Unfortunately, the few published estimates of mycorrhiza biomass are difficult to evaluate owing to differences in separation methods, phenological status of the stand at sampling, stand types, depth of soil sampled, and whether "active" or total mycorrhiza weights are reported (Fogel 1980). The main problems are sampling efficiency and assessing the physiological status of mycorrhizae. The sampling problem arises from the small size of hydrated mycorrhiza fragments, ranging in size from 0.5 to 3.0 mm in length and 0.15 to 0.6 mm in diameter with an average dry weight per fragment of 0.043–0.197 mg (Fogel 1980; Lyford 1980; Vogt *et al.* 1980). The constraints imposed by the fragility (Lyford 1980) and size of mycorrhizae require that an efficient sampling scheme recover all organic matter larger than 0.15 mm in size, not just mycorrhizae remaining attached to roots. This implies that soil crumbs should be dispersed and that efficiency can be improved by concentrating the organic fraction by wet sieving or by other means. These limitations indicate that hand sorting of roots, direct observation of untreated soil samples, and use of large mesh soil screens may result in an underestimate of mycorrhiza biomass.

Assessing the physiological status of mycorrhizae is important in determining the contribution of mycorrhizae to ecosystem processes, but reporting only "active" mycorrhizae biomass may result in an underestimate of their contribution. Common criteria for characterizing "active" mycorrhizae include: turgidity, color, association with mycelia, hyphal strands, or rhizomorphs, and when sectioned, color of root tissues (Harvey *et al.* 1976). Generally, no attempt is made to differentiate between "inactive" and dead mycorrhizae, or state what proportion of the total mycorrhiza biomass is "active." Underestimates of "active" mycorrhiza biomass may result from the difficulty in classifying the physiological status of mycorrhizae and in handling samples. For example, exposure to dry air for only a few minutes is sufficient to make small roots shrivel and die (Lyford 1975).

Given the aforementioned limitations in the reported

TABLE 1. Percent stand total allocation, throughput, and uptake of organic matter (in kilograms per hectare) in a young Douglas-fir ecosystem, Dinner Creek, Oregon

	1976–1977			1977–1978		
Component	Standing crop	Throughput	Uptake	Standing crop	Throughput	Uptake
Tree						
Foliage	14 736(3)	2 410(8)	2 716(7)	15 042(3)	2 949(9)	3 330(6)
Branches	30 475(6)	270(1)	969(2)	31 174(6)	2 091(6)	872(2)
Bole	263 282(51)	138(<1)	7 000(17)	270 144(51)	138(1)	8 707(15)
Roots	67 395(13)	0	5 704(14)	76 214(14)	3 788(12)	13 016(23)
Mycorrhizae	25 023(5)	14 611(50)	15 261(37)	26 739(5)	14 967(46)	18 102(32)
Total tree	400 911(78)	17 429(59)	31 650(76)	419 313(79)	23 933(74)	44 027(78)
Forest floor						
<2 mm	6 970(2)	2 355(8)	2 410(6)	7 025(2)	2 375(7)	2 949(5)
2–25 mm	6 564(1)	420(1)	270(1)	6 414(1)	411(1)	2 091(4)
>25 mm	5 500(1)	ND[a]	138(<1)	5 683(1)	ND	138(<1)
Total forest floor	19 034(4)	2 775(9)	2 818(7)	19 122(4)	2 786(8)	5 178(9)
Fungi						
Sclerotia	2 785(1)	2 158(7)	2 131(5)	1 911(1)	1 204(4)	865(2)
Sporocarps	65(<1)	65(<1)	65(<1)	55(1)	55(1)	55(1)
Hyphae						
Litter	369(<1)	296(<1)	164(<1)	385(<1)	297(<1)	324(<1)
Soil	6 666(1)	6 695(23)	4 781(12)	5 483(1)	4 156(13)	6 129(11)
Total fungi	9 885(2)	9 214(31)	7 141(17)	7 834(2)	5 712(18)	7 373(13)
Soil organic matter	87 600(17)	ND	ND	87 600(16)	ND	ND
Stand total	517 430(100)	29 418(100)	41 609(100)	533 869(100)	32 431(100)	56 578(100)

[a] ND = no data.

estimates of mycorrhiza biomass, there are no published data available for direct comparison with the Dinner Creek results. Indirect comparisons can be made, however, by making certain assumptions. Lyford (1975), for instance, obtained an average of 1141, mostly mycorrhizal, root tips per cubic centimetre of forest floor in a 70-year-old mixed hardwood stand by teasing apart 1-cm cubes under a stereomicroscope. If one assumes each root tip weighs 0.1 mg (reported averages range from 0.043 to 0.197 mg), the resulting biomass of 45 640 kg · ha^{-1} is nearly twice as large as the standing crop of mycorrhizae at Dinner Creek. Another bit of evidence derives from a recent study by Vogt *et al.* (1980) of 23- and 180-year-old stands of *Abies amabilis* (Dougl.) Forbes (Pacific silver fir). The maximum seasonal standing crops of "active" mycorrhizae are ca. 2000 kg · ha^{-1} in the 23-year-old stand and 2700 kg · ha^{-1} in the 180-year-old stand (estimated from Fig. 3 in Vogt *et al.* 1980); no estimates of total mycorrhiza or fine-root (<2 mm) biomass are presented. If the proportion of "active" mycorrhizae at Dinner Creek (7.95 ± 2.09%) is used to estimate a total standing crop of active, inactive, and dead mycorrhizae, the 23-year-old stand has a standing crop of ca. 25 157 kg · ha^{-1} and the 180-year-old stand ca. 33 962 kg · ha^{-1}. These estimates compare very well with the Dinner Creek estimates of 25 023 and 26 739 kg · ha^{-1} (Table 1). The combined standing crops of mycorrhizae and fine roots (<5 mm) in year 1 of 30 952 kg · ha^{-1} and in year 2 of 39 833 kg · ha^{-1} at Dinner Creek are much larger than Santantonio's (1979) estimates of fine-root biomass in 70- and 170-year-old stands of Douglas-fir in western Oregon. If mycorrhizae are excluded from the comparison, Santantonio's (1979) annual mean values of 4.9 to 5.8 t · ha^{-1} of fine roots compare favorably to the Dinner Creek average in year 2 of 6.7 t · ha^{-1}; the Dinner Creek average was much smaller, 3.2 t · ha^{-1}, during year 1, possibly due to the drought. Assuming that the sites are roughly comparable ecologically, this may indicate that our wet sieving technique is more efficient than hand sorting and (or) dry sieving methods.

The question arises of how the mycorrhiza standing crop at Dinner Creek can be two to four times larger than that of fine roots. One possible explanation is the prolific branching of many mycorrhizae, and the small biomass of roots needed to connect these clusters to larger roots. Lyford (1975) counted 1786 mycorrhizal root tips on a 44-mm-long root axis of paper birch

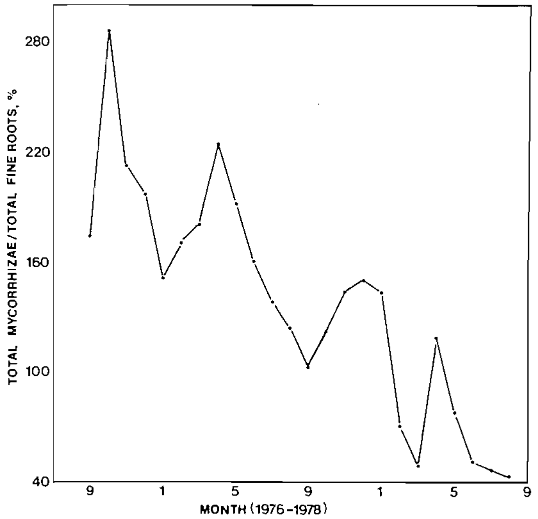

FIG. 2. Proportion of mycorrhizal to total fine-root biomass in the top 1 m of soil in the Dinner Creek, Oregon, stand.

and 588 root tips on a 19-mm-long axis of red oak, with an average of 47 root tips per 10 mm of linear roots and 227 tips per 10 mm of roots with clusters of mycorrhizae. If root tips average 0.2 mm in length (0.2–0.5 mm *fide* Lyford 1975) the root-tip length will average 9.4 per 10 mm of linear roots and 45.4 mm on roots with clusters. These estimates do not include mycorrhiza fragments dislodged during processing or detached during root senescence.

In both years of the study, mycorrhizae comprised the largest proportion of the weight of fine roots in the fall and again in the spring (Fig. 2). Mycorrhizae account for the smallest proportion of fine roots during the summer and late winter. Vogt *et al.* (1980) report the largest proportion of "active" mycorrhiza to fine-root biomass occurs during the fall and winter months when snow covers the forest floors in their Pacific silver fir stands. They did not have a spring peak in the proportion of mycorrhizae, perhaps owing to differences in the phenology of subalpine and low-elevation sites, species differences, or the frequency of their sampling. The proportion of mycorrhizae to fine roots at Dinner Creek (Fig. 2) varies from a low of 124% to a high of 286% in year 1 and in year 2 from a low of 43% to a high of 151%. The decreased proportion of mycorrhizae during year 2 is caused by a twofold increase in the biomass of fine roots. Extension of nonmycorrhizal lateral roots in response to better environmental conditions during year 2 may account for the increased proportion of fine roots.

Organic matter uptake

Uptake or organic matter production is dominated by trees (Table 1). Total tree uptake ranged from 76% of total stand uptake in year 1 to 78% in year 2. Mycorrhiza production comprises 41–48% of tree uptake, with the remainder apportioned among boles, 19–22%; roots, 18–30%; foliage, 8–9%; and branches, 2–3%. Fungal uptake, excluding mycorrhizae, is 1.4 to 2.5 times that of the forest floor. Soil hyphae account for 67–83% of fungal uptake, with the remainder allocated among sclerotia, 12–30%; litter hyphae, 2–4%; and sporocarps, 1%. Soil organic matter uptake was not measured.

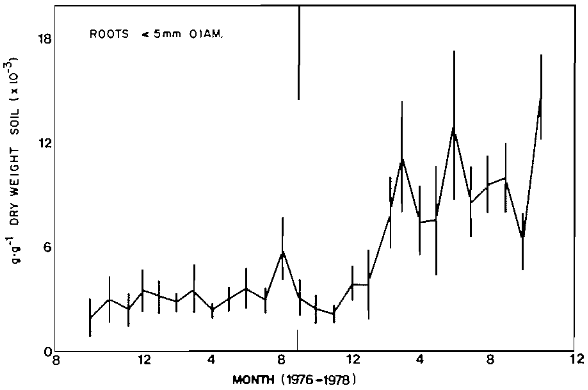

FIG. 3. Monthly changes in nonmycorrhizal fine-root standing crop in the top 12 cm of soil in the Dinner Creek, Oregon, stand (mean plus 95% confidence interval).

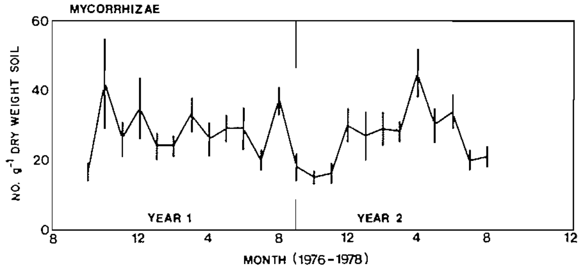

FIG. 4. Monthly changes in the standing crop of mycorrhizae in the top 12 cm of soil in the Dinner Creek, Oregon, stand (mean plus 95% confidence interval).

The severe drought in the fall of year 1 may have suppressed fine-root production (Fig. 3). The only significant increase in fine-root standing crop (uptake 4050 kg · ha^{-1}) during year 1 occurred in August 1977. Fine-root standing crop in year 2 decreased during the late summer of 1977 (throughput 3789 kg · ha^{-1}), rapidly increased to a level twice that of year 1 (uptake 10 953 kg · ha^{-1}), and then dropped to a low in October of the 3rd year. The decrease in the standing crop during the summer of 1978, while significant, did not reach the minima measured in the summers of 1976 and 1977.

The drought during year 1 may also have suppressed mycorrhiza production as indicated by the lack of a

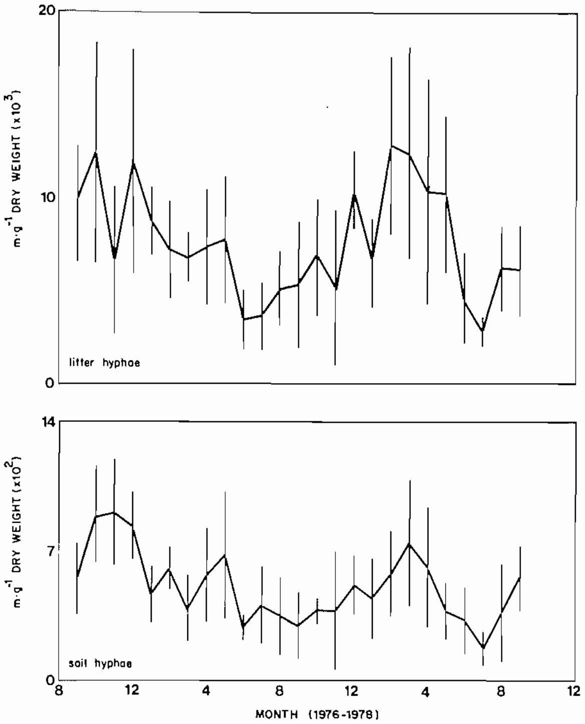

FIG. 5. Monthly changes in the standing crops of soil (0- to 5-cm depth) and litter hyphae in the Dinner Creek, Oregon, stand (mean plus 95% confidence interval).

peak in the standing crop during the spring of 1976 (Fig. 4). The standing crops measured in August and October of 1976 are significantly larger than in the months preceding, although the large error associated with the October point results in its not being significantly different from most of the winter and spring points. The October point is significantly different than the August 1976 point, however. The August 1977 peak in mycorrhiza standing crop during year 1 also occurs in the fine-root data (Fig. 3). Low mycorrhiza standing crop during the summer dry period is repeated in all three summers (Fig. 4); these levels are not significantly different. Vogt *et al.* (1980) report a seasonal pattern of mycorrhiza levels in Pacific silver fir similar to that of Dinner Creek during year 2. They noted that the lowest seasonal biomass of "active" mycorrhizae occurred during the summer and the highest levels during fall and winter. Summer moisture stress (−0.5 bars) did not reach a level that they felt could have affected the production of mycorrhizae and ascribed decreased root activity to fewer carbohydrates being available to root systems during periods of rapid shoot growth. Moisture stress at Dinner Creek definitely reached levels (−13.5 bars in September 1977 and −9.9 bars in September 1978) affecting tree growth, although the general decreases in total mycorrhiza standing crop during the spring and early summer may reflect decreased carbohydrate supply coupled with active decomposition or consumption of mycorrhizae.

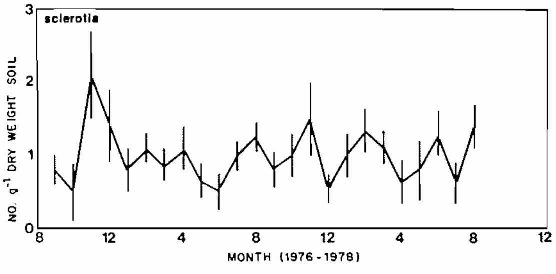

FIG. 6. Monthly changes in the standing crop of sclerotia in the top 12 cm of soil in the Dinner Creek, Oregon, stand (mean plus 95% confidence interval).

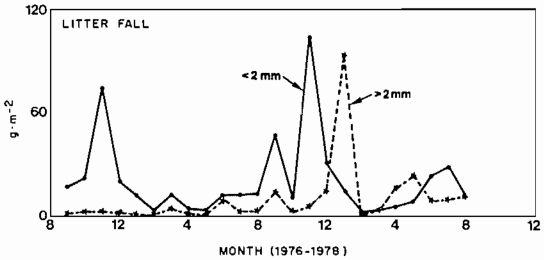

FIG. 7. Monthly inputs of fine (<2 mm) and woody litter to the forest floor at Dinner Creek, Oregon.

Organic matter throughput

Trees dominate throughput of organic matter (release or return to forest floor and soil). Total tree throughput ranged from 59% of total stand throughput in year 1 to 74% in year 2 (Table 1). Fine roots and mycorrhizae account for the bulk of tree throughput (Table 1) ranging from 84% in year 1 to 78% in year 2. Mycorrhiza throughput is three to five times larger than throughput resulting from litter decomposition and is four times larger than fine-root throughput during year 2 when precipitation was near normal. No measurable fine-root throughput occurred in year 1 during the drought. Decomposition of fine litter (<2 mm) accounts for 85% of forest floor throughput and is two to three times larger than fungal throughput. Soil hyphae comprise 73% of fungal throughput (Fig. 5), followed by sclerotia, 21−23% (Fig. 6); litter hyphae, 3−5%; and sporocarps, 1%.

A sharp increase in branch throughput, from 270 to 2091 kg · ha^{-1}, and a smaller increase in foliage throughput, from 2410 to 2949 kg · ha^{-1}, occurred during the 2nd year (Fig. 7). The increased litter fall measured during year 2 may be related to the drought during the 1st year of the study. Storm-induced branch pruning was probably delayed by the drought followed

TABLE 2. Mean nutrient concentrations (percent) in ecosystem components, Dinner Creek, Oregon (standard deviations in parentheses)

Component	N	P	K	Ca	Mg
Foliage					
Crown	1.440(0.159)	0.190(0.006)	0.483(0.051)	0.595(0.033)	0.290(0.017)
Base	1.157(0.024)	0.133(0.003)	0.387(0.031)	1.393(0.048)	0.177(0.004)
Senescent	0.559(0.022)	0.144(0.012)	0.236(0.033)	0.998(0.102)	0.113(0.009)
Branch					
Crown	0.691(0.045)	0.115(0.008)	0.997(0.059)	0.542(0.028)	0.205(0.013)
Base	0.497(0.038)	0.082(0.030)	0.645(0.061)	1.240(0.125)	0.116(0.009)
Senescent	0.155(0.006)	0.007(0.000)	0.037(0.015)	0.427(0.032)	0.030(0.026)
Bole minus bark	0.065(0.017)	0.004(0.001)	0.015(0.007)	0.043(0.007)	0.006(0.003)
Bark	0.019(0.003)	0.026(0.008)	0.093(0.007)	0.411(0.027)	0.038(0.003)
Roots					
>5 mm[a]	0.083	0.007	0.039	0.158	0.007[b]
<5 mm	0.544(0.141)	0.102(0.013)	0.199(0.038)	0.494(0.050)	0.071(0.012)
Mycorrhizae					
Mixed	0.622	0.147	0.205	0.144	0.002
Tuberculate	1.608	0.258	0.950	0.057	0.115
Hysterangium sp.	0.749	0.138	0.405	7.830	0.241
H. crassum[c]	0.523(0.023)	0.137(0.012)	0.267(0.035)	6.267(2.297)	0.317(0.015)
Forest floor					
<2 mm	0.685(0.174)	0.084(0.020)	0.102(0.034)	0.828(0.178)	0.170(0.098)
>2 mm					
class 1	0.159(0.022)	0.005(0.002)	0.027(0.006)	0.120(0.035)	0.014(0.005)
class 2	0.014(0.001)	0.0003(0.0001)	0.0014(0.0003)	0.008(0.002)	0.0008(0.0001)
class 3	1.066(0.085)	0.027(0.006)	0.123(0.015)	0.738(0.150)	0.074(0.015)
Fungi					
Hyphae[c]	2.217	0.141	0.024	0.659	0.221
Sporocarps	2.882(0.694)	0.540(0.146)	3.866(1.605)	0.038(0.034)	0.097(0.029)
Sclerotia	0.961(0.083)	0.215(0.045)	0.199(0.040)	0.787(0.133)	0.118(0.021)
Soil					
0–20 cm	0.148(0.016)	0.060(0.017)	0.311(0.138)	0.168(0.066)	0.612(0.192)
20–40 cm	0.101(0.041)	0.053(0.012)	0.308(0.137)	0.094(0.050)	0.658(0.168)
40–60 cm	0.069(0.027)	0.045(0.014)	0.342(0.124)	0.076(0.044)	0.588(0.299)
60–80 cm	0.055(0.019)	0.051(0.012)	0.370(0.133)	0.040(0.034)	0.668(0.190)
80–100 cm	0.039(0.017)	0.048(0.013)	0.379(0.151)	0.031(0.035)	0.674(0.324)

[a] Data for roots 20–50 mm in diameter from Santantonio *et al.* (1977).

[b] R. Fogel (unpublished data).

[c] Stark (1972).

by a larger than normal branch throughput in the subsequent storms of year 2 (Fig. 1).

Unfortunately, we were unable to measure the throughput of large roots (more than 5 mm in diam.) and soil organic matter. The lack of these data may not seriously affect the results of our study, however. Several investigators studying other tree species have been unable to detect any significant seasonal differences in the standing crop of large roots (Heikurainen 1957; Edwards and Harris 1977; Persson 1978). The reported turnover time of soil organic matter in a New Zealand pasture soil is 63 years (O'Brien and Stout 1978). If this value is used to calculate soil organic matter throughput at Dinner Creek, the result is 1391 kg · ha^{-1} · year^{-1} or about 4–5% of the total stand throughput.

The annual throughput values of 0–29% of maximum fine-root standing crop and 56–58% of mycorrhiza standing crop at Dinner Creek are similar to previous estimates. Annual throughputs of 80–92% of the root biomass have been reported for fine roots of European beech (Göttsche 1972), 30–40% for Douglas-fir (Lyford 1975; Santantonio 1979), 42% for *Liriodendron* (Edwards and Harris 1977), 90% for walnut (Bode 1959), and 48% for an oak woodland (Ovington *et al.* 1963). These larger reported values indicate throughput of fine roots at Dinner Creek might be even greater under normal environmental conditions when the stand is not enduring or recovering from a severe drought.

Recent research on the turnover of organic material extracted densimetrically also provides indirect evi-

TABLE 3. Percent stand total nutrient stocks (in kilograms per hectare) in biomass, forest floor, and soil at Dinner Creek, Oregon, 1976–1977

Component	Organic matter	N	P	K	Ca	Mg
Tree						
Foliage[a]	14 736	171	20	57	205	26
Branches, live[b]	22 768	113	19	147	282	26
Branches, dead	7 707	12	1	3	33	2
Bole, bark	32 010	6	8	30	132	12
Bole, wood	231 272	150	9	35	100	14
Roots, coarse[c]	61 466	51	4	24	97	4
Roots, fine	5 929	32	6	12	29	4
Mycorrhizae[d]	25 023	156	37	51	36	1
Total	400 911	691(9)	104(2)	359(1)	914(12)	89(1)
Forest floor						
<25 mm	13 534	93	11	14	110	22
>25 mm	5 500	<1	<1	<1	<1	<1
Total	19 034	93(1)	11(<1)	14(<1)	110(1)	22(<1)
Fungi						
Hyphae, litter	369	8	1	<1	2	1
Hyphae, soil	6 666	147	9	2	44	15
Sclerotia	2 785	27	6	6	22	3
Sporocarps	65	2	<1	3	<1	<1
Total	9 885	184(2)	16(<1)	11(<1)	68(1)	19(<1)
Soil						
0–20 cm		1961	811	4 229	2262	8 315
20–40 cm		1852	992	5 789	1746	12 363
40–60 cm		1337	888	6 772	1498	11 638
60–80 cm		889	835	6 068	650	10 953
80–100 cm		579	720	5 685	463	10 109
Total	87 600	6618(88)	4246(97)	28 543(99)	6619(86)	53 378(100)
Stand total	517 430	7586(100)	4377(100)	28 927(100)	7711(100)	53 508(100)

[a] Calculated using elemental content of needles from crown base.
[b] Calculated using elemental content of branches from lower crown.
[c] Calculated using values for 20–50 mm broad roots from Santantonio *et al.* (1977) and R. Fogel (unpublished data) for Mg content.
[d] Calculated using elemental content of mixed living and dead mycorrhizae.

dence that the magnitude of the turnover of roots and mycorrhizae at Dinner Creek is reasonable. Spycher *et al.* (1982) observed an increase in light fraction organic material (<1 mm in diam.) from March to June at the 5- to 15-cm depth of ca. 38 t · ha^{-1} in a western Oregon Douglas-fir stand. The annual turnover of fine roots, mycorrhizae, and soil hyphae for the same soil depth at Dinner Creek was 10.6 t · ha^{-1} in year 1 and 13.3 t · ha^{-1} in year 2.

Net primary production

Total net primary production (NPP) increased from 49 079 kg · ha^{-1} in year 1 to 67 960 kg · ha^{-1} in year 2. Belowground NPP by roots and mycorrhizae comprised a major proportion of total NPP, 72.5% in year 1 and 73.4% in year 2. Data from the Pacific silver fir stands studied by Vogt *et al.* (1980) provide supporting evidence for a large throughput of organic matter below ground (Grier *et al.* 1981). In the 23-year-old stand, 60.4% of the total stand NPP was below ground and 71.8% in the 180-year-old stand. About 60% of the total NPP of a 14-year-old Scots pine in Sweden is invested in the growth and maintenance of the root system (Ågren *et al.* 1980). Mycorrhizae dominated belowground NPP at Dinner Creek during the 1st year (84%) when no detectable throughput of fine roots occurred. During the 2nd year when the production of roots was twice that during year 1, the contribution by mycorrhizae dropped to 66% of belowground NPP. Mycorrhizae were also the major contributors to total NPP representing 61 and 49% in years 1 and 2, respectively.

Biomass increment by woody tissues comprised 59% of the aboveground NPP in year 1 and 53% in year 2. Bole biomass increment contributed most to aboveground NPP (52 and 48%, respectively) during both years. Aboveground detritus production was dominated by foliage in year 1 (86%) and by foliage (57%) plus branches (40%) in year 2. Total biomass increment for both above- and below-ground tree components required 65% of the NPP in both years.

Nutrient concentrations

Table 2 gives nutrient concentrations used in calculating nutrient stocks, uptake, and throughput. The concentrations at Dinner Creek are similar to those previously reported (Fogel 1976; Gessel and Turner 1976; Sollins *et al.* 1980; Vogt and Edmonds 1980). Nutrient concentrations of needles and branches from the base of the canopy were used in all calculations since canopy position influences nutrient concentration (Lavender and Carmichael 1966). Soil chemical analyses indicated decreasing concentrations of N and Ca with depth and no substantial change in concentration of P, K, and Mg with depth.

The nutrient analysis of 2500 randomly picked mycorrhiza fragments was used in calculating mycorrhizal nutrient stocks, uptake, and throughput. This mixed sample consisted almost entirely of "dead" or "inactive" fragments. Additional analyses were done on "active" tuberculate mycorrhizae and on mycorrhizae plus associated rhizomorphs from a *Hysterangium* sp. mat for comparison. Nutrient concentrations of the "active" tuberculate mycorrhizae were higher than the mixed sample for all elements analyzed, except Ca. *Hysterangium* mycorrhizae appear to be unique in having a very high concentration of Ca.

Nutrient concentrations of fungal rhizomorphs reported by Stark (1972) were used in determining nutrient stocks, uptake, and throughput for hyphae and are probably conservative. Flanagan and Van Cleve (1977) report N concentrations of 5.32 and 4.72% and P concentrations of 0.55 and 0.20% for field-collected mycelium and rhizomorphs, respectively. Laursen and Miller (1977) report slightly lower N concentrations of 1.6–3.8% for hyphae grown in liquid Nobel's medium.

Nutrient stocks

Table 3 indicates that the soil contains the single largest pool of all nutrients studied, 86 to ca. 100% of a given element. Trees contain from 69 to 94% of the nutrients not in the soil pool, forest floor, 4–17%; and fungi, 3–19%. Similar allocations of nitrogen have been reported for a number of forest ecosystems (Fogel 1980). Nutrient stocks in the aboveground tree components exceed by 1.2 to 8.9 times those in the belowground tree components. Roots and mycorrhizae contain larger stocks than either the forest floor or fungi of all nutrients except Ca.

Although foliage contains larger quantities of N and K than any other single tree component, woody tissues *in toto* contain larger percentages of the total stocks in trees (71–84%) for all nutrients studied. Stocks in aboveground woody tissues also exceed those in foliage. Belowground stocks of N, P, and K in roots and mycorrhizae are larger than those in foliage; stocks of Mg and Ca are smaller. The percents of tree stocks contained in belowground components range from 35 to 45% for N and P; but Mg, Ca, and K are present in much lower percentages (10–24%). Roots and mycorrhizae differ strikingly in both concentration and quantity of nutrient elements: stocks of N and P in mycorrhizae greatly exceed those in roots, but roots contain about the same quantities of K and larger quantities of Ca and Mg.

Nutrient stocks in soil hyphae, except K, exceed those in other fungal components. Sclerotia contain larger quantities of K than sporocarps, soil hyphae, or litter hyphae. Potassium is the only nutrient in sporocarps representing a significant share (27%) of the total fungal nutrient stock.

Nutrient throughput

Annual throughputs for all elements studied are presented in Table 4. Large differences exist in the relative order of allocation of throughput among ecosystem compartments between years 1 and 2, in marked contrast to the allocation of organic matter and nutrient stocks. The contribution of trees to nutrient throughput was slightly higher in year 2 (1.2–1.4 times), except for Mg which increased from 14% of stand throughput in year 1 to 30% in year 2. Contributions of the forest floor to throughput are minor, ranging from 5 to 22% of total throughput for each element, while the percent contribution during both years was about equal. The contribution by fungi to throughput in year 2 was about half that in year 1 owing to the small throughput of hyphae and sclerotia.

Foliage completely dominates the aboveground return of nutrients to the forest floor. Even in year 2 when branch detritus was 71% of foliage detritus, the contribution of woody litter to nutrient throughput was minor. At best, woody litter contained 30% of the Ca and Mg in foliage throughput. Aboveground throughput of all elements in year 2, except for P, increased by 33–50% over the levels in year 1 reflecting the 82% increase in detritus production and more importantly the 22% increase in throughput of nutrient-rich foliage.

The relative rate of flow of nutrients through the forest floor can be expressed as residence time and turnover rate, which vary considerably among nutrient elements in the Dinner Creek forest floor (Table 5). Residence time is defined as the mass of organic material or nutrient elements in the forest floor divided by the annual litter fall input (MacLean and Wein 1978). The reciprocal of the residence time, expressed as a percent, is the fraction of the nutrient stock involved in the annual flux, the fractional annual turnover. A primary assumption of these calculations is that the forest

TABLE 4. Percent stand total release and return of nutrients (in kilograms per hectare) associated with organic matter throughput at Dinner Creek, Oregon

Component	N	P	K	Ca	Mg
	September 1976 – September 1977				
Tree					
Foliage	14(5)	4(9)	6(13)	24(18)	3(11)
Branches	<1	<1	<1	1(1)	<1
Bole	<1	<1	<1	1(1)	<1
Total aerial	14(5)	4(9)	6(13)	26(20)	3(11)
Roots, coarse	<1	<1	<1	<1	<1
Roots, fine	0	0	0	0	0
Mycorrhizae	91(30)	22(51)	30(63)	21(16)	1(<1)
Total tree	105(35)	26(60)	36(75)	47(35)	4(14)
Forest floor	19(6)	2(5)	3(6)	23(17)	5(18)
Fungi	178(59)[a]	15(35)	9(19)	63(47)	19(68)
Stand total	302(100)	43(100)	48(100)	133(100)	28(100)
	September 1977 – September 1978				
Tree					
Foliage	17(6)	4(10)	7(13)	29(20)	3(13)
Branches	3(1)	<1	1(2)	9(6)	1(4)
Boles	<1	<1	<1	1(1)	<1
Total aerial	20(8)	4(10)	8(15)	39(28)	4(17)
Roots, coarse	<1	<1	<1	<1	<1
Roots, fine	20(8)	4(10)	8(15)	19(13)	3(13)
Mycorrhizae	93(35)	22(54)	31(56)	22(16)	<1
Total tree	133(50)	30(73)	47(86)	80(56)	7(30)
Forest floor	19(7)	2(5)	3(6)	23(16)	5(22)
Fungi	113(43)	9(22)	5(9)	39(28)	11(48)
Stand total	265(100)	41(100)	55(100)	142(100)	23(100)

[a] The value of 74 kg · ha^{-1} published in Fogel (1980) resulted from using a N concentration value (0.622%) for hyphae instead of the value (2.21%) published by Stark (1972).

floor nutrient stock is in steady state on an annual basis, accumulation equals decomposition losses. The forest floor is not in steady state at Dinner Creek (net increase from year 1 to year 2 was 88 kg · ha^{-1} of organic matter), but the residence time and fractional annual turnover have been calculated because: (*i*) they allow a general comparison with stands in other regions and (*ii*) they allow comparisons among values for nutrients and organic matter. The mobility series derived from the residence times is K $>$ P $\geq$ Ca $>$ N $>$ Mg, which is similar to the mobility series for forest floors in *Pinus banksiana* Lamb. (MacLean and Wein 1978). Phosphorus and Ca are more mobile than in most hardwood stands (Lousier and Parkinson 1978). A mobility series similar to that of Dinner Creek, but with N and Mg reversed, has been reported for Douglas-fir needles confined in litter bags in western Washington (Edmonds 1979). In general, N and Mg have residence times in the same range as organic matter at Dinner Creek, while P and K are considerably shorter, and Mg slightly shorter. The low ratios of the residence times to that for organic matter indicate an apparently tight circulation for all of the elements studied. Residence times of all elements, except P, were shorter during year 2 when there was an increase in litter input (foliage and branch throughput).

Aboveground throughput is minute, however, compared with the belowground release of N, P, and K by trees. Throughput of these elements by roots and mycorrhizae ranges from 83 to 87% of total tree throughput and comprise about half (45–51%) of the Ca and Mg released in year 2. Mycorrhizal throughput accounted for all of the belowground nutrient release during year 1 owing to the lack of measurable fine-root throughput. Consequently, Mg release was negligible in year 1 owing to the very low concentration of Mg in mycorrhizae. During year 2, mycorrhizal throughput was four to five times greater than roots for N, P, and K, nearly equal for Ca, and three times less for Mg. Harris *et al.* (1980) estimate that the annual return of elements to soil by root processes (death and decomposition, exudation, leaching) in a *Liriodendron tulipifera* L. stand is six times (recalculated from their Table 1) the combined aboveground inputs (precipitation, litter fall, canopy leaching) for K and at least 1.5 times aboveground inputs for N. Our data suggest, ignoring inputs in precipitation, exudation, and leaching, that return to the soil by mycorrhizae and roots is six to

TABLE 5. Residence times[a] and fractional annual turnover[b] of organic matter and mineral elements in the forest floor at Dinner Creek, Oregon

	Residence time (years)						Fractional annual turnover (%)					
Year	OM[c]	N	P	K	Ca	Mg	OM	N	P	K	Ca	Mg
1	6.8	6.6	2.8	2.3	4.2	7.3	15.0	15.1	36.4	42.9	23.6	13.6
2	3.7	4.7	2.8	1.8	2.9	5.8	27.3	21.5	36.4	57.1	34.8	17.4

[a] Residence time = $T_n = \dfrac{\text{forest floor stock}}{\text{annual litter input}}$

[b] Fractional annual turnover = $\dfrac{1}{T_n} \times 100$.

[c] OM = organic matter.

TABLE 6. Percent stand total nutrient uptake (in kilograms per hectare) at Dinner Creek, Oregon

Component	N	P	K	Ca	Mg
	September 1976 – September 1977				
Tree					
Foliage	31(10)	4(9)	11(16)	38(22)	5(18)
Branches	3(1)	1(2)	4(9)	8(5)	1(4)
Bole	5(2)	<1	2(3)	6(4)	<1
Total aerial	39(13)	5(11)	17(27)	52(31)	6(21)
Roots, coarse	1(<1)	<1	1(1)	3(2)	<1
Roots, fine	22(7)	4(9)	8(11)	20(12)	3(11)
Mycorrhizae	95(31)	22(49)	31(44)	22(13)	<1
Total tree	157(51)	31(69)	57(84)	97(57)	9(32)
Forest floor	17(6)	2(4)	3(4)	23(14)	5(18)
Fungi	133(43)	12(27)	8(11)	50(29)	14(50)
Stand total	307(100	45(100)	68(100)	170(100)	28(100)
	September 1977 – September 1978				
Tree					
Foliage	39(10)	4(7)	13(14)	46(20)	6(17)
Branches	4(1)	1(2)	5(5)	10(5)	1(3)
Bole	5(1)	<1	2(2)	7(3)	1(3)
Total aerial	48(12)	5(9)	20(21)	63(28)	8(21)
Roots, coarse	2(1)	<1	1(1)	3(1)	<1
Roots, fine	60(15)	11(19)	22(23)	54(23)	8(23)
Mycorrhizae	113(28)	27(47)	37(39)	26(11)	<1
Total tree	223(56)	43(75)	80(84)	146(63)	16(46)
Forest floor	20(5)	4(7)	8(9)	39(16)	4(11)
Fungi	153(39)	11(19)	6(6)	50(21)	15(43)
Stand total	396(100)	58(100)	94(100)	235(100)	35(100)

seven times aboveground inputs for K and for N. Inclusion of N and K dissolved in precipitation, measured in an old-growth stand by Sollins *et al.* (1980), changes the ratios slightly at Dinner Creek to 4.3 times aboveground inputs for K and 5 to 6 times for N.

Nutrient uptake

The relative order of nutrient uptake by ecosystem components was essentially the same during both years of study (Table 6). Trees dominated nutrient uptake by utilizing 51–84% of the total stand uptake of N, P, K, and Ca. In year 1, tree uptake of Mg was 32% of stand uptake, slightly less than the 50% share for fungi. In year 2, tree and fungal uptake of Mg were nearly equal, 43 and 46%, respectively. Fungi accounted for most of the remaining nontree uptake of all elements; forest floor uptake was relatively unimportant. Percent of stand uptake by trees occurred in the order: K > P > Ca ≥ N > Mg. The percent of stand uptake by fungi was in the reverse order of that by trees: Mg > N > Ca ≥ P > K. The order of nutrient uptake by the forest floor was not consistent between years 1 and 2, although Mg and Ca represented a larger share of stand uptake than did the other elements.

Nearly all of the aboveground nutrient uptake was utilized in foliage production. The remaining uptake of N, Ca, and Mg was divided about equally between uptake by branches and boles. The nonfoliage uptake of P and K was nearly all utilized in branch production. Aboveground uptake of all nutrients in year 2 increased over year 1 by 19–21%, for N, K, and Ca, by 33% for Mg, and no increase for P.

Belowground uptake of N, P, and K in root and mycorrhiza replacement (production) ranged from 70 to 88% of total tree uptake. Belowground uptake of Ca ranged from 46 to 57% of total tree uptake while uptake of Mg by the belowground components was 33% of uptake in year 1, when fine-root production was nil, and then increased to 50% in year 2. Mycorrhiza production utilized the largest share of the belowground uptake of N, P, and K. Fine roots dominated belowground uptake of Mg during both years. Ca uptake by fine roots was slightly less than uptake by mycorrhizae in year 1 but was nearly twice as large in year 2.

The studies at Dinner Creek provide further evidence, beyond that arising from studies including fine roots, of the major contribution made by the belowground ecosystem to nutrient cycling in temperate forests. Fine roots and mycorrhizae account for the bulk of the total stand throughput (50–58%) and uptake (51–55%) of organic matter. These large fluxes in the production, senescence, and decomposition of organic matter are accompanied by similar fluxes in N, P, and K. Fluxes in other ecosystem components account for most of the cycling of Ca (fungi, foliage) and Mg (fungi, foliage, and forest floor).

While the importance of roots and mycorrhizae in nutrient cycling is very striking, further refinement of the estimates is needed. The few studies on the contribution of roots and mycorrhizae to ecosystem processes only provide a rough approximation of their importance because of the difficulties in distinguishing active and inactive roots. Data is lacking, for instance, on changes in nutrient content during the production, senescence, and decomposition of mycorrhizae. The higher concentrations of N, P, and K in tuberculate mycorrhizae compared with the mixed mycorrhiza sample (Table 2) suggest that a substantial portion of the nutrients present in active mycorrhizae are withdrawn by the tree before senescence of mycorrhizae. If withdrawal of nutrients from senescing mycorrhizae occurs, fewer nutrients would need to be supplied by the soil for tree uptake. Further refinement of our understanding of this and other belowground processes hinges on accurately distinguishing between active and inactive mycorrhizae.

The present approaches of measuring either "active" or total mycorrhiza biomass are inadequate because they: (*i*) make comparison among different studies difficult, if not impossible; (*ii*) underestimate throughput because steady state conditions are assumed and death is not taken into account; and (*iii*) make it impossible to estimate production by balancing quantitative changes in the biomass of live and dead mycorrhizae over time. Morphological criteria previously used to classify "active" mycorrhizae identify a small proportion of the total biomass (ca. 8% at Dinner Creek) and may produce an underestimate of production given the large, inseparable biomass of "inactive" and dead mycorrhizae. Some attempt should also be made to measure the efficiency of various methods for estimating fine-root and mycorrhiza biomass. Wet sieving, for instance, produces higher values of nonmycorrhizal fine roots (0.4–3 mm diam.) than excavation in radiata pine stands (Moir and Bachelard 1969). In addition, Reynolds (1970) has shown that wet sieving with a 0.53-mm screen recovers a third more roots than does a 0.91-mm screen. The probable impact of the drought at Dinner Creek indicates that studies of the belowground ecosystem require sampling over several years.

Answering these and other questions has the potential of greatly changing our understanding of ecosystem structure and function. The potential is especially promising when the answers are coupled with our knowledge of biochemical mechanisms controlling root growth, environmental and ecologic factors controlling ion-uptake rates by mycorrhizal fungi, and the factors controlling movement of water, minerals, and energy sources within trees.

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